A NEW *TEMPSKYA* FROM KENT

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A NEW *TEMPSKYA* FROM KENT

By M. E. J. CHANDLER

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SYNOPSIS

A silicified specimen with well-preserved cell structure, found on the shore at Sheppey, proves to be a new species of the Mesozoic " genus " *Tempskya* in which individual solenostelic stems are welded together into a " false stem " by their intertwining roots. Detailed morphology links this specimen most closely with *Tempskya grandis* from the Upper Cretaceous of Wyoming but the two are distinguished by the greater number of meristeles normally present within the rhizome section of the American species and the great difference of size.

The type of siliceous preservation suggests that the specimen may have come from the Woolwich Beds of Herne Bay.

The Kent *Tempskya* is only the second species to be recorded from England and is quite distinct from the well known *Tempskya erosa* found in the Wealden Beds and the Lower Greensand.

INTRODUCTION

Some years ago a member of the United States Geological Survey, Dr. R. A. Scott, paid a visit to the Sheppey coast to see this famous source for London Clay plants. He picked up, lying loose on the shore, a somewhat waterworn " stem " and kindly gave it to the British Museum (Natural History). A transverse cut just below the apex of the specimen (V.51841) showed that it was a fern beautifully preserved in silica with excellent cell structure. The siliceous preservation raised the question of the origin of this plant so unlike the London Clay fruits and seeds which are commonly pyritized, occasionally carbonaceous or with calcitic internal casts and not infrequently a mixture of pyrites and carbonaceous tissues. The specimen has now been studied and the results of the investigations are described below.

DESCRIPTION OF SPECIMEN

The silicified " false stem " was originally about 12·5–13 cm. long. The cutting process when the apex was severed of course involved some loss of length. Both parts of the specimen have now been examined, further cuts have been made, and a few thin sections have been prepared. The specimen is now in four fragments. The poorly preserved basal part is numbered V.51841, the central part V.51841*a*; and the apex, which has further been cut longitudinally into two fragments, V.51841*b* and *c*. Of the six slides (V.51841*d–i*), V.51841*d* from the top of V.51841 is too ill-preserved to be very informative or worth thinning. V.51841*e* and *f* are from the upper surface of V.51841*a*, the slide *e* being lower than *f*. Slides V.51841 *g*, *h* and *i* come from the base of V.51841*b*. They do not extend across the whole breadth of the specimen nor even of the cut surface of V.51841*b*, but all three together with *b* 1 and 2 lie within about 10 mm. of the length of the " stem ".

The transverse diameter of the whole specimen at broadest (i.e. at about the middle) is 5.4 by 3.5 cm. In its rolled and waterworn state it shows superficially a complex of stems with general longitudinal alignment and some evidence of dichotomous bifurcation and intertwining, (Pl. 1, figs. 1, 2). Remains of a few projecting scattered petiole bases are seen (Pl. 1, fig. 2; Pl. 2, fig. 4). Section V.51841*f* passes through one stem in the early stages of dichotomous division (Pl. 1, fig. 3; Pl. 3, fig. 6; Pl. 4, fig. 7) so that there are two steles but both are still surrounded by a single cortex and epidermis which have become somewhat bilobed. The whole specimen is more abraded on one broad surface than on the other. Some crushing, dislocation and disintegration can be detected in the section towards this worn side making the structures more obscure here than elsewhere. There has been some disruption of the stele, for example, in the dividing stem (Pl. 3, fig. 6; Pl. 4, fig. 7). A few deep concavities show the surface view of ramentae in lighter coloured silica (Pl. 1, fig. 1). They are obscured by abundant freely branching roots many of which grew upwards. The fringed edges of the scales, due to their multi-cellular structure, show clearly in places. Despite wear and tear the specimen appears to retain, approximately at least, the original length and breadth, for emerging petiole bases project from the general surface both on the side and at the apex. The structure, at the lower end where amorphous silica has obliterated cell tissues, is more obscure than in the upper two-thirds of the specimen. More especially is this the case on the less well preserved side.

In transverse section in the upper part (Pl. 1, fig. 3) all or part of seven radially arranged dorsiventral stems are visible. They show a typical solenostelic structure. Five of them are closely adjacent to or actually at the circumference; two are more deeply embedded but still radially aligned. In all, the steles are towards the inner end of a radial line, and the leaf traces or meristeles at their outer ends. The spaces between the stems are packed closely with ramentae and roots of various sizes. The latter may be sectioned longitudinally for a short distance but are commonly transversely or obliquely cut in the slides and cut surfaces. The penetrating roots which pierce the scales and weave in and out weld the stems into the " false stem ". The solidity of the whole complex is undoubtedly enhanced by the process of silicification which unites stems, scales and roots into a solid inseparable mass, silica penetrating all tissues and replacing cell contents just as in *Osmunda dowkeri*.

The maximum transverse diameter of the component stems is about 15.5 by 9 mm., or 15 by 11 mm. in the middle of the specimen, larger, some 22 to 25 by 11 mm., in the basal part. Near the apex some stems are smaller, 12 or 13 by 8 mm., but others are 15 by 13 and 16 by 11 mm.

In addition to the roots which belong to the fern itself, numerous " foreign " roots are visible in the sections. In particular they are concentrated in an irregular but continuous thin belt of sclerenchyma outside, concentric with and close to the steles and meristeles. They make this belt of tissue very conspicuous while often obscuring its detailed structure. They are also abundant in the sclerenchyma of the pith adjacent to the leaf gaps (Pl. 5, fig. 8; Pl. 7, fig. 10; Pl. 8, fig. 11; Pl. 10, fig. 13). Some of these roots may be monocotyledonous, others dicotyledonous, as they show radially arranged small xylem cells containing large scattered vessels. I am indebted to Dr. Holttum for these suggestions. The roots sometimes take the place of the stelar tissues of the fern roots within a dense belt of surrounding sclerenchyma.

Structure of individual stems. The stems are clearly solenostelic. Some sections show a complete cylinder with no leaf gap (Pl. 8, fig. 11), others show a single leaf gap (Pl. 7, fig. 10; Pl. 9, fig. 12). Yet others have two leaf gaps (Pl. 5, fig. 8; Pl. 6, fig. 9). The pattern due to the development of the leaves is repeated at regular intervals in the individual stems so that the sections made at different levels across the false " stem " show successive changes. In any single section the included stems are commonly at different stages in development. Intermediate stages have been seen on the polished surfaces exposed both before and after section cutting but being unsuitable for photography they are not represented in the plates.

The periphery of the stems, inside an ill-preserved epidermis from which the ramentae arise, is formed of several layers of opaque sclerenchymatous cells with dark contents. Up to a dozen layers have been counted. Exactly similar outer tissues are described by Read & Brown (1937 : 110) in *Tempskya grandis* as the " outer cortex ". Within is a layer of sclerenchyma, at least twenty cells thick, cells which although thick-walled retain a considerable lumen. It clearly corresponds with the " middle or sclerenchymatous cortex " in *T. grandis*. Individual cells are isodiametric in cross section where the walls appear to be unevenly patchily thickened. Inside again occurs a thick layer, twenty or more cells thick, of thin-walled parenchyma (corresponding to the " inner cortex " of *T. grandis*). It is at least as broad as and may be broader than the middle sclerenchymatous cortex. Almost invariably the individual cells show black rounded objects occupying much of the cavity; sometimes these objects themselves lie in a rounded cavity within the cell. Under the quarter-inch lens most of them appear to be agglomerated crystals, although a few simple crystals are seen. In longitudinal sections of the cells they appear as clumps of elongate crystals with their long axes at right angles to the longer axes of the cells. Similar inclusions occur sparsely in the sclerenchyma of the middle cortex. Towards the inner margin of the parenchymatous zone there is always a continuous narrow band of sclerenchyma very irregular in thickness and therefore in outline as seen in transverse section. It may be sharply delimited from the parenchyma in which it lies by a dark line on the outer side, (Pl. 5, fig. 8; Pl. 8, fig. 11; Pl. 9, fig. 12), but less sharply from three or four layers of parenchyma cells which lie between it and the stele. These innermost parenchyma cells are rather small but display the same crystalline inclusions. They also occur abundantly in the irregular sclerenchyma belt just described, a belt seen only in *T. grandis* among the well preserved fossil species and in the less well preserved *T. superba* Arnold.

The stele is bounded both externally and internally by an endodermis and associated tissues. In places the endodermis is well defined as a single layer of equiaxial cells. Inside it, preserved only in certain places, are two or more layers of tangentially elongate thin-walled cells with clear cavities (Pl. 11, fig. 14). They probably represent pericycle and phloem but no sieve plates appear to be preserved. The xylem varies considerably in thickness from about three tracheids in depth to sixteen or twenty as a result of leaf trace formation. Along the margins of the xylem are patches of very small tracheids, some certainly showing scalariform thickening. The bulk of the xylem is composed of conspicuous large metaxylem tracheids with multiseriate thickening which causes them to appear angular in transverse section so producing a characteristic pattern. Where roots are about to arise the small elements at the margin become more numerous causing an outward bulge in the endodermis. It is probable that some of these are protoxylem but no spiral thickening appears to be preserved. A considerable amount of parenchyma, often with crystalline inclusions is scattered among the tracheids, again as in *T. grandis*. *T. rossica* and *T. wesselii* also show this feature (Andrews & Kern 1947 : 147) as does *T. superba* (Arnold 1958 : 137). Where the stele becomes thin and the bulge which initiates a leaf trace begins to form, the metaxylem tracheids follow a tangential course (Pl. 10, fig. 13). In the actual slide they then show the thickening clearly. At one leaf gap the end of the stele abutting on it shows what appear to be some spiral tracheids near the margin of the xylem.

Where the pith within the stele adjoins the endodermis there is a thin layer of parenchyma with the usual inclusions. It is continuous through the leaf gap with the fine parenchyma which bounds the stele externally. Otherwise almost the whole pith is formed of sclerenchyma with thick-walled cells, and, at the centre, with little lumen (Pl. 5, fig. 8; Pl. 7, fig. 10). The sclerenchyma is also continuous through the gap with the sclerenchyma of the cortical zone of the rhizome.

Scales or Ramentae. These may be very broad. One which could be measured is at least 10 mm. wide. The elongate cells which form them lie end to end and side to side. In the rows of cells the end walls are transverse or oblique to the length. The cell rows diverge towards the lateral margins of the scales where the free ends of the rows separate and form the characteristic fringed edge. Seen in transverse section of the stems they appear as thin multicellular plates of tissue (Pl. 2, fig. 5; Pl. 7, fig. 10).

Development of leaf traces and structure of meristele. On that side of the stele towards the circumference of the " false stem ", leaf gaps arise at short longitudinal intervals indicating that the leaves must have been crowded. In a single section across one stem two and sometimes three leaf-traces may still be included within the cortex and epidermis showing that they arise at acute angles (Pl. 3, fig. 6, stem *b*; Pl. 9, fig. 12). Once they have emerged from the stem they apparently change their direction and pass out of the " false stem " quickly. An occasional projecting leaf base on the side of the upright " false stem " (Pl. 1, fig. 2) points to the fact that they were borne at intervals along its length. A terminal crown may also have occurred (Pl. 2, fig. 4). The appearance of the stele in transverse section varies with the degree of development of the leaf trace, the positions of the leaf gaps and meristeles in successive sections suggesting that they were borne in two somewhat irregular rows. The stages in trace formation have been pieced together from the various stems in thin sections and cut surfaces. Serial sections were not attempted because there is only one specimen and its preservation is so patchy. This caused the sections to break irregularly and made complete transverse slices difficult to obtain. It also limited the amount of thinning that could be carried out.

Development of a trace is heralded first by the thinning of part of the stele connected with its formation while simultaneously an adjacent protuberance occurs (Pl. 6, fig. 9, rhizome *a*; Pl. 7, fig. 10). The bulge or protuberance then develops a pair of angular thickenings on the inside of the stele near its inner limits (Pl. 3, fig. 6, rhizome *b*). Further thinning at the inner ends of the bulge just beyond the thickened angles now produces a gap, first on one side and then on the other (Pl. 7, fig. 10). As a result a C-shaped trace opening inwards is separated from the stele (Pl. 9, fig. 12; cf. Pl. 6, fig. 9, rhizome *a* with Pl. 7, fig. 10). The trace passes upwards and outwards through the cortex. The angles on the inner side of the stele soon become elongated tangentially and approach one another fusing as they pass up the stem with resulting restoration of the complete cylinder.

At certain stages of development two gaps are seen in a single transverse section. In this case a semicircular section of the stele with its flattened surface towards the periphery of the " false stem " gives rise to thin outward curving lobes at its angles. The lobes separate first from the central area remaining attached at their inner ends and so producing a double convex curve on each side, the curve of the developing trace being much shorter than that of the parent stele. The central fragment of stele which may be simple or bilobed then appears as an island separated from the main stele by two developing leaf gaps (Pl. 5, fig. 8; Pl. 6, fig. 9, stem *b*). Usually one trace becomes detached as on the right in Pl. 6, fig. 9, while the other still remains attached although much thinned and ready for almost simultaneous separation.

Recently emerged leaf traces soon form elongate bulges on the stem surface even prior to their complete departure from it (Pl. 5, fig. 8, cf. *m* in Pl. 7, fig. 10 and in Pl. 9, fig. 12). The final separation of the trace as it passes through the cortical tissues next occurs. A tongue of sclerenchyma grows inward between stem and trace, one side giving off a branch which enters the bay of the meristele. Sclerenchyma from the opposite side also extends inwards until the two sides meet thereby completely surrounding both stem and leaf base (*m* in Pl. 7, fig. 10). At a slightly higher level the outermost stem tissues grow in also and divide sclerenchyma of stem and leaf base so that they completely part company (*p* in Pl. 7, fig. 10) the trace continuing upwards and outwards until it emerges at the surface of the " false stem ".

In shape the meristele becomes markedly incurved as it passes out of the stem (contrast the three meristeles in Pl. 9, fig. 12) while simultaneously its ends thicken. As is to be expected, the succession of tissues is as in the stem itself. The meristele may be only one or two tracheids thick at the middle of the arc but there are up to about seven at the incurved ends. Endodermis and associated tissues completely surround it. Owing to the angle at which traces arise transverse sections cut them somewhat obliquely so that the tissues appear blurred. The thin parenchyma which completely encircles the stele of the leaf trace and its irregular sclerenchyma is continuous with the parenchyma of the stem until separated by the ingrowing of the sclerenchyma. As in the stem the cells of this tissue show the characteristic crystalline inclusions.

An unexplained peculiarity is seen in the meristele of one thin section. Some of the tissues, more especially the parenchyma cells, have broken down and in their place oval opaque black bodies can be seen. Similar structures in a root of *Tempskya knowltoni* from Montana are described and figured by Seward (1924 : 494, pl. 17, fig. 24). He was unable to explain them but suggested that they might be coprolites of a small insect or possibly escaped cell contents. Certainly in the Kent specimen each such body occupies a separate cell until the surrounding cell walls have actually broken down. Seward adds that entomologists he consulted were unable to identify the bodies with the activities of any known boring animal and no trace of any insect had been found. " They consist ", he stated, " of finely comminuted plant debris or dark masses of rounded cell contents and are certainly not spores ".

The roots (Pl. 2, fig. 5). These vary greatly in size and are branched repeatedly. Some are as much as 2 mm. broad. Many roots and their branches grow upward through the tissues. They show a small stele with typical diarch arrangement, a well-defined endodermis surrounding it. There are about four to six large metaxylem tracheids, flanked at opposite poles by groups of about three to six small protoxylem tracheids. The metaxylem tracheids may be 0·027 mm. or less in diameter. Phloem is rarely preserved. Outside the endodermis are several layers of concentrically arranged sclerenchymatous cells with well developed cavities. They are succeeded further out by a thick band of dense sclerenchyma with cavities obliterated. In transverse section these cells appear both radially and concentrically aligned forming a very conspicuous band of tissue which may be 0·3 mm. broad. It corresponds to the " middle cortex " of Andrews & Kern in their description of *Tempskya* (1947 : 139). In young roots the sclerenchyma may be less dense. Sometimes outside the sclerenchyma there is another concentric belt of thin-walled cells of about the same width (Andrews' " outer cortex "). It is not invariably preserved. In Pl. 2, fig. 5, the " outer cortex " has a lozenge or diamond-shaped outline of which half only is preserved. This shape is dictated by the pressure of closely compacted masses of roots in the spaces between the stems. In some roots only the sclerotic tissue survives surrounding an empty circular space, occasionally occupied by foreign tissues as described above.

Affinities. The composite character of this " false stem " with its dichotomous solenostelic true stems embedded in a mass of their own roots and scales connects the specimen with the Mesozoic *Tempskya* of Corda (1845 : 81). Kidston & Gwynne-Vaughan (1911 : 13) later published a generic diagnosis of the genus quoted by Read & Brown (1937 : 108). Unfortunately the true relationship to living ferns has not yet been discovered although many distinguished botanists have carried out research on the subject. As long ago as 1872 Feistmantel suggested that *Tempskya* was not a genus but a mode of preservation of several distinct types of fern stems. To the writer, this view appears to be greatly strengthened by the occurrence of a supposed Mesozoic genus in the Tertiary. Read & Brown (1937 : 120) discuss the taxomic affinities and summarize views published prior to their paper. They created the " family " Tempskyaceae as the natural affinities could not be discovered but probably no such family exists. It is merely a convenient way of grouping different ferns with a similar habit. Dr. R. E. Holttum and Dr. T. G. Walker have kindly examined slides or detailed photographs of the Kent fern but were unable to recognize any living genus with which there is complete agreement. It is necessary to remember that the appearance of these plants in life may have differed materially from that when fossilized thanks to the cementing and hardening effects of silicification welding stems and roots into an apparently solid entity. Like Feistmantel, Andrews & Kern (1947 : 143) consider that the " trunk " of the genus " represents a peak of structural evolution that is manifest in a generally comparable fashion in a number of ferns, both living and fossil ". They refer to scattered references in literature, not quoted in detail, to living ferns having an upright trunk composed of branching stems " held together to a greater or lesser degree by a mass of adventitious roots ". Among these are, of course, some of the well-known tree ferns with a similar upright trunk or caudex which differ in important respects from *Tempskya* and all of which are certainly much larger than the Kent specimen. Writing later Andrews (1961 : 116) after briefly describing the genus commented that the radial development suggests a single stem in the early sporeling stage which grew and divided to form a large and longer trunk. He did not then consider the anatomy of the stem sufficiently distinctive to afford evidence of affinity but again emphasized that the mode of growth could have arisen independently in several unrelated groups. None known to him agreed closely with *Tempskya* either in detailed anatomy or in the huge number of stems involved. The smaller size of the Kent " false stem " with its fewer true stems strongly suggests that this specimen may eventually be matched among living material when sufficient knowledge of the anatomy and cytology of this vast group of plants is available and allowance is made for the profound alteration in appearance due to silicification. Whatever the relationship of the Mesozoic species may be it is most likely that the Kent specimen belongs to a living genus. Naturally Recent root stocks and stem bases are not available in unlimited amount or variety. The majority of *Tempskya* species are from America which has produced at least seven distinct kinds. Some of these are enormous attaining to 16 in. in diameter and a height of at least 12 or possibly 19 or 20 feet. Some include a very large number of stems. Thus Andrews & Kern (1947 : 155) quote more than 200 stems in a single trunk. Some of the American species are well preserved and fall into two clear groups (Read & Brown 1937 : 119; Andrews & Kern 1947 : 147). The Kent " stem " closely agrees in its detailed morphology with *T. grandis* Read & Brown (1937 : 114, pl. 29, fig. 2; pl. 32, figs. 2–5; pl. 33, figs. 1–4; pl. 34, figs. 1–4; pl. 35, figs. 1–4; pl. 41, fig. 4; pl. 42, figs. 1–3; pl. 43, figs. 1, 4–7) which belongs to the first of these groups. It is an Upper Cretaceous species from the Aspen shales of Wyoming. It is about 8 cm. in diameter and some 20 cm. long, perhaps larger because more mature than the Kent fossil. Despite its somewhat worn appearance, so that one or two of its stems are abraded longitudinally on the outer side, it looks as if the whole " trunk " approximated closely to the original dimensions for the reasons given on p. 172. The increased abundance of roots near the base and the failure of preservation of other detail in the basal part suggests that this is near to the true base of the specimen which, must, therefore, have been on a much smaller scale than other known species.

Summarizing points of resemblance, some of which have been mentioned in the description, the Kent *Tempskya* and *T. grandis* have in common: xylem containing an appreciable amount of parenchyma; an inner parenchymatous cortex which encloses a constant but narrow irregular band of sclerenchyma close to but not contiguous with the stele; a similar narrow zone of parenchyma forming the outer layers of pith in contiguity with the stele and with the sclerenchyma inside; large individual stems in the false " stem " with rather short internodes. Thus apart from difference of size which may not necessarily be of great significance the material of the Kent specimen can only be distinguished from *Tempskya grandis* by the smaller number of meristeles in the transverse sections of the rhizomes. It has from one to three, commonly two meristeles, whereas in *T. grandis* there are two to five, commonly three or four, implying greater crowding of the leaves in this latter species (cf. Read & Brown 1937 : 115, text-fig. 3, pl. 28, fig. 2 [Note the erratum slip]; pl. 32, figs. 2–5; pl. 33, figs. 1–4).

T. superba described by Arnold (1958 : 138) has suffered obliteration of much detail by complete silicification of the tissues. Form and size of individual stems are retained and there is enough structure to show a strong resemblance to *T. grandis* in that both have the distinctive continuous but irregular sclerotic layer in the inner cortex absent in other species except the Kent form. All three also have scleren-. chyma in the pith. Arnold separates *T. superba* from *T. grandis* partly on the much larger size of its stems which he gives as at least 1 cm. in diameter without attached leaf bases, 2 cm. if they be included. He infers that the diameter of *T. grandis* (stems) is 6–7 mm. but according to measurements based on Read & Brown's figures the two species appear to approach one another in this respect, while in the Kent *Tempskya* a considerable range of size occurs in the one specimen depending on the position within the length of the stem (cf. p. 172). Size of stem alone, therefore, does not appear to be a sufficient reason for separation. The holotype of *T. grandis* is 8 cm. in diameter, 20 cm. long. That of *T. superba* was a slab measuring about 6 by 12 cm., 2 cm. thick before cutting. It was obviously very incomplete. Both greatly exceed the dimensions given for the Kent specimen (see p. 172). *T. superba* normally shows four or five foliar traces (meristeles) in each stem section, indicating, as in *T. grandis* exceptionally short internodes. On the grounds of number of foliar traces it therefore appears that the *Tempskya* from Kent is distinct from these two species which otherwise it closely resembles in detailed cytology. *T. superba* was found in an eroded Oligocene deposit in Nebraska but is believed to have been derived from the Lower Cretaceous Dakota Sandstone.

As only one specimen from Kent is in existence it is merely described as *Tempskya* sp. It is the second species to have been discovered in England. A much earlier record is *T. erosa* Stokes, Webb & Mantell from the Wealden Beds or Lower Greensand of Tilgate Forest, Hastings and Potton. *T. erosa* differs completely in its character and preservation from *Tempskya* sp. described here. Its numerous much smaller stems show little structure in detail but are embedded in dense masses of innumerable roots. It has been re-described and discussed by Stopes (1915 : 16) and more recently illustrated by Seward (1924, pl. 16, fig. 4; pl. 17, fig. 16). It is so different in every way that it does not concern us here any further.

Origin of the Specimen. As soon as the specimen was referred to *Tempskya* it raised the question whether a supposed Mesozoic form found at Sheppey could have come from the London Clay, especially in view of the silicious preservation (see p. 171). Mr. G. F. Elliot has pointed out that a similar preservation is known in Palm and dicotyledonous wood, in *Osmunda dowkeri* and in cones of *Pinus macrocephalus* from Herne Bay. *Pinus macrocephalus* is occasionally picked up on the shore between Bishopstone and Reculvers where the Thanetian outcrop is exposed. Some of the above have been attributed to the Thanet Sands, others to the London Clay but their preservation is different from that of *Tempskya* except in the case of the dicotyledonous woods from Herne Bay. A few of these (B.M.N.H., V.27923) which have closely comparable and characteristic preservation have come from unweathered foreshore outcrops of the Woolwich Bottom Bed in Herne Bay. Material washed out of the Thanet Sands has been found well to the west of Herne Bay hence *Tempskya* could have been transported naturally to the beach at Sheppey. To summarize, the preservation suggests that the Lower part of the Woolwich Beds at Herne Bay is the most likely source of the specimen. The difficulty of accepting such a source is eliminated if, as seems probable, such a habit of growth is not confined to the Mesozoic

The photographs were taken in the Photographic Department of the British Museum (Natural History). The typing was done by Mrs. M. Firth. To all the persons concerned and to those already mentioned in the text the author's warmest thanks are given.

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DESCRIPTION OF PLATES

Note. The photographer has taken Pl. 1, fig. 3 and Pls. 3–5 from the back of the slide. Allowance must be made for this mirror image when examining the plates in order to study the development of the stele and leaf traces in the rhizomes.

PLATE 1

Tempskya sp.

FIGS. 1, 2. " False stem " from opposite sides. The apex has been removed. V.51841, upper surface of fragment so numbered. Position of slides is at *f*, *g–i*. On the left in Fig. 1 dichotomous forking of the small stems is seen. The white hollow at base shows scales in the actual specimen and upwardly directed roots. In Fig. 2 rounded projections at *p*. are much abraded petiole bases. × 1 approx.

FIG. 3. Transverse section of " stem" somewhat crushed and disorganized in the lower half. Seven numbered true stems are visible (part only preserved of 1 and 3), 2 and 7 are embedded in roots and scales of " stem " so do not in this section touch the surface of the specimen. 4 is in process of dichotomous division, 5 and 6 are rather poorly preserved. × 2. V.51841*f*.

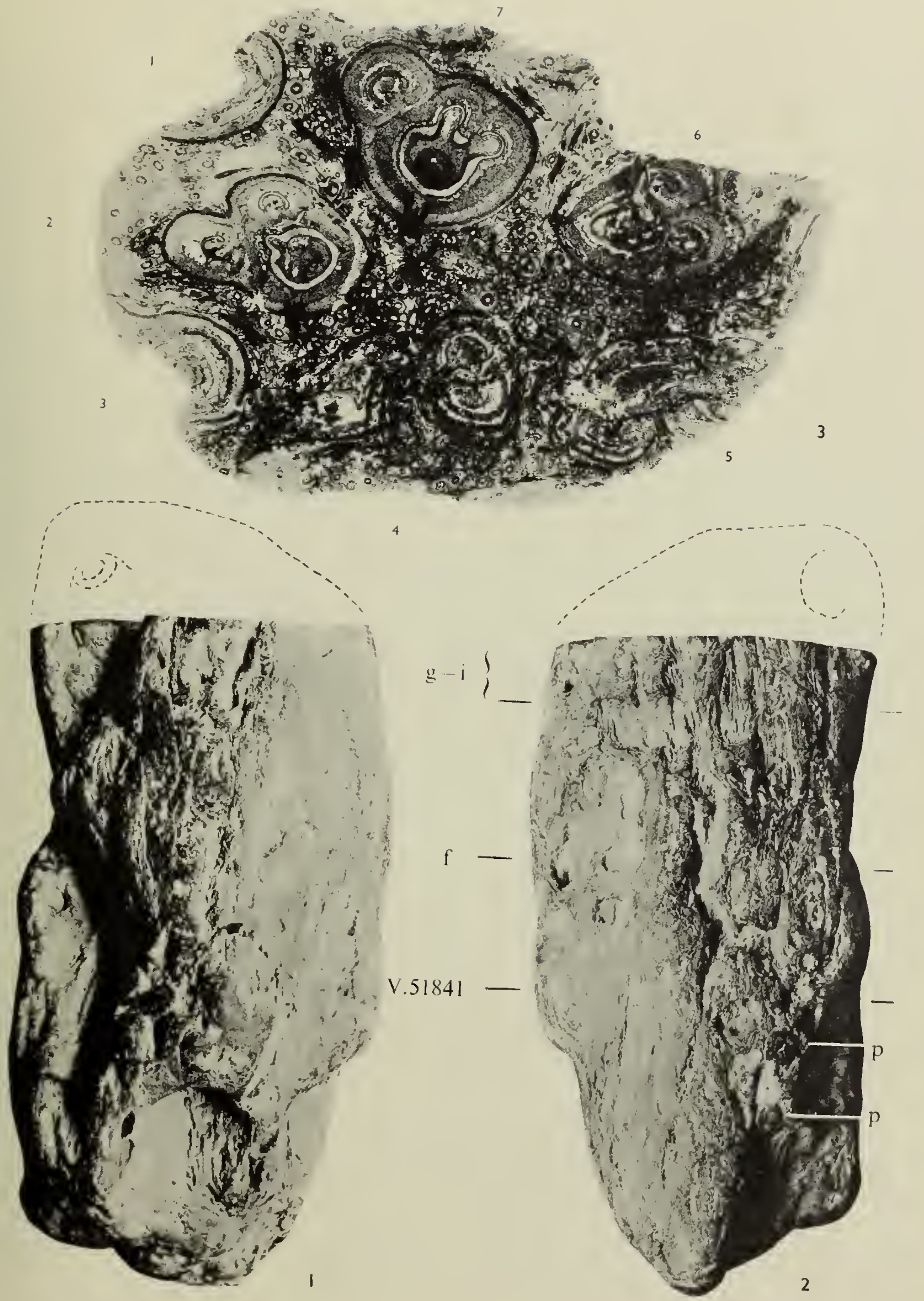
1
2
3
4
5
6
7
3
g–i
f
V.51841
p
p
1
2

PLATE 2

***Tempskya* sp.**

FIG. 4. Side of severed apical fragment showing projecting petioles at *p*. Fragment cut longitudinally on right in preparing other sections but here shows only roots and scales out of focus. ×2. V.51841*b*.

FIG. 5. Transverse section of typical diarch root penetrating scales arising from the epidermis of a stem. Large metaxylem tracheids occupy centre of root and are flanked by two patches, at opposite poles, of small protoxylem tracheids. Tissues outside xylem, including endodermal ring, decayed (white in figure). Next come three concentric and radial rows of sclerenchyma, *sc*, with cavities. Outside again are four to five rows of dense sclerenchyma cells, *d*, with blocked cavities. A diamond-shaped area (left half only preserved) of thin-walled cells beyond the sclerenchyma is cortex, *c*. The multicellular character of scales, *s*, can be seen obscurely (out of focus). ×*ca* 90. V.51841*i*.

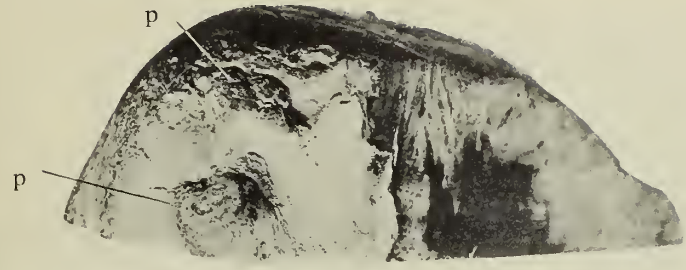

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PLATE 3

Tempskya sp.

Fig. 6. Part of slide V.51841*f* shown in Plate 1, fig. 3. The mass of roots and scales in which the stems are embedded are sectioned in various directions. Stem *b* (2 in Pl. 1, fig. 3) shows a typical cylindrical stele with protuberance on the left marking initiation of a leaf trace. Detached meristeles of two incipient leaf-bases are also seen. Stem *a*, (7 in Pl. 1, fig. 3) shows a stele with two leaf gaps one each side of a small island of xylem. Two curved arms of stele indicate leaf traces not yet severed. A stem at *c* (4 in Pl. 1, fig. 3) which has begun to divide dichotomously is, in consequence, bilobed. It is outlined in white but is shown untouched and more highly magnified in Pl. 4, fig. 7. The obscure appearance is caused by the partial decay and dislocation on this side of the " stem " but the two new steles are already separated. ×5·5.

9

PLATE 4

Tempskya sp.

Fig. 7. The dividing stem in Pl. 3, fig. 6 (the right margin of the figure just cuts the edge of the stem). Originally a cylinder the stele on the right has been crushed and consequently dislocated in four places. One break passes through the prominence on the left which indicates the beginnings of a leaf trace. A meristele which has already separated is seen (surrounded by white) below the stele. The second stele in the left lobe of the dichotomy is also distorted but, again, the lobe (dislocated) of an incipient leaf trace is visible (above white patch). ×10. V.51841*f*.

1

PLATE 5

Tempskya sp.

FIG. 8. The join on the right was due to the stem lying in part on two negatives.

Stem *a* in Plate 3, fig. 6. Dark band at base crossing cortex and epidermis is a root. The two leaf gaps flanking the island of stele are better seen here as are the curved incipient meristeles on each side. The curved loop on the left is almost separated but that on the right is still fully attached. A deeply curved leaf-trace (top left) is about to emerge. It is already partially cut off from the parent stem by ingrowing sclerenchyma from the two sides. Both parent stele and meristele are partly embraced externally by an irregular band of sclerenchyma much infested with " foreign " roots. This belt of tissue is surrounded by parenchyma on both sides. ×10. V.51841*f*.

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PLATE 6

Tempskya sp.

Fig. 9. Stems *a*, *b* and in part *c* show a later (younger) stage of these stems in Plate 3 (reversed as in a mirror). The stele bounding one leaf gap (in *a*) has now united again with the central island of xylem and forms the loop for a new meristele. The meristele on the left in Pl. 3 has separated and moved out into the cortex (right in Pl. 6). The other leaf gap still persists. In *b* the bulge seen on the left in Pl. 3 has separated from the stelar ring (on right in Pl. 6); the angular thickenings flanking the bulge in Pl. 3 have elongated and united, but two new loops have formed, one on each side of the bilobed fused xylem from which they have severed themselves at their upper ends thereby producing two curved loops and two leaf gaps. The lower limb in Pl. 6 has just separated from the stem stele. In *c* the formation of another stele is visible. ×5. V.51841*g*.

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PLATE 7

Tempskya sp.

Fig. 10. A yet higher level in stem *a*. The loop in Pl. 6, top left, has now formed a new meristele. The gap in the stele of the stem still persists but another loop at the end of the lower free limb is about to initiate another meristele. The leaf trace (top right) is now free from the parent stem and is surrounded by its own epidermis. The successive cortical coats (see p. 173) are well marked. The irregular sclerenchyma belt within the parenchyma around the stele is little infested with " foreign " roots here, less so than in the young meristele (centre, above). The scales arising from the epidermis are well preserved but the magnification is insufficient to show the multicellular structure. ×10. V. 51841*h*.

10

PLATE 8

Tempskya sp.

FIG. 11. Stem *b* at a higher level than in Pl. 6, and differently oriented. The meristele of Pl. 6 has separated from the stem and is not shown in this section. The bilobed island of stele in Pl. 6 has reunited with the arms of the main stele from which the incipient meristeles, there seen as curved extremities, have here separated and moved outwards. The upper of these two meristeles is now partly separated from the stem stele by the ingrowing of the outermost band of sclerenchyma. " Foreign " roots are clearly shown in the pith sclerenchyma and in that outside the main stele itself. The narrow loop of a new meristele is seen on the radius between the two separated meristeles. ×10. V. 51841*i*.

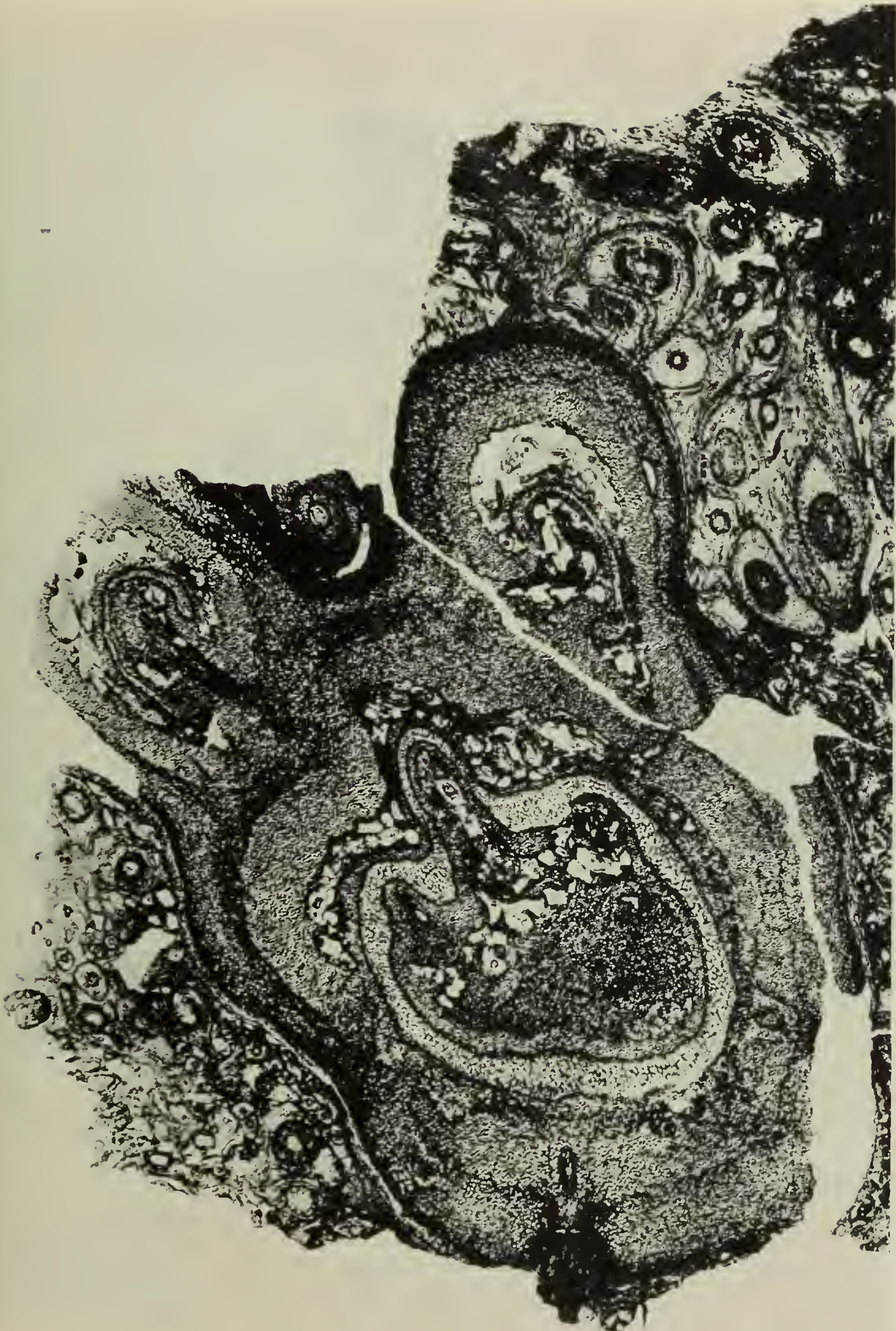

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PLATE 9

Tempskya sp.

FIG. 12. A higher section through stem *a*. The loop in the stele in Pl. 7 has separated to form a meristele leaving a new leaf gap while the gap seen in Pl. 7 has closed. The curved hook-like free end of the stem stele in Pl. 7 has passed out as a meristele (right, below) partially separated by ingrowing sclerenchyma. The meristele above in Pl. 7 is now almost separated from the parent stem as is evident from the constriction which has formed on each side of it and the thick sclerenchyma between the two. The separated trace in Pl. 7 has grown right out of the " false stem ". The successive coats: epidermis with thin outer cortex, sclerenchymatous middle cortex, thick parenchymatous inner cortex with included irregular band of sclerenchyma just outside the stele but separated from it by parenchyma, are clearly seen. × 10. V.51841*i*.

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PLATE 10

Tempskya sp.

FIG. 13. An arc of the stele in Pl. 8. It shows the large metaxylem tracheids with scattered patches of parenchyma among them. Small tracheids are seen at the lower angle of the thickened part of the stele above which, to the right, transverse orientation of tracheids is apparent where a leaf gap is in process of development. Parenchyma cells with black crystalline inclusions are seen in the inner cortex, and these cells abut on the stele on both sides. Thick-walled sclerenchyma with small cavities shows clearly in the centre of the pith but is largely obscured by " foreign " roots in the irregular sclerenchyma belt of the inner cortex outside the stele and, in places, in the pith. ×35. V.51841*i*.

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PLATE 11

Tempskya sp.

Fig. 14. Stelar arc on the opposite side of the stele in Pl. 8. Sclerenchyma cells of the irregular band are seen at *sc* in the parenchymatous inner cortex where " foreign " roots are absent. Small marginal tracheids are well developed in the south-east corner of the stele and especially where roots are in process of formation. Tangential cells associated with endodermis are visible on the right. Other features as in Pl. 10. ×35. V.51841*i*.

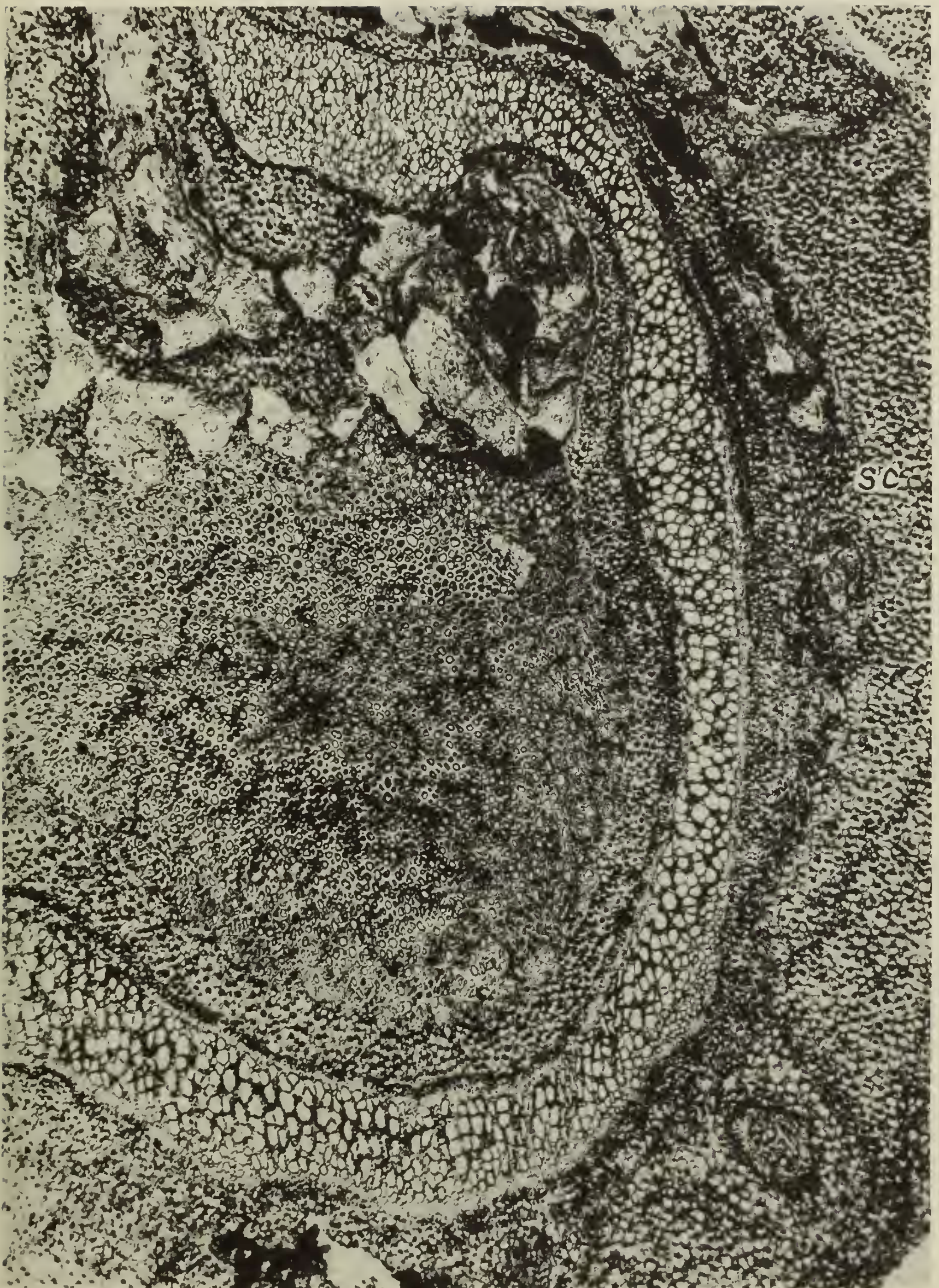

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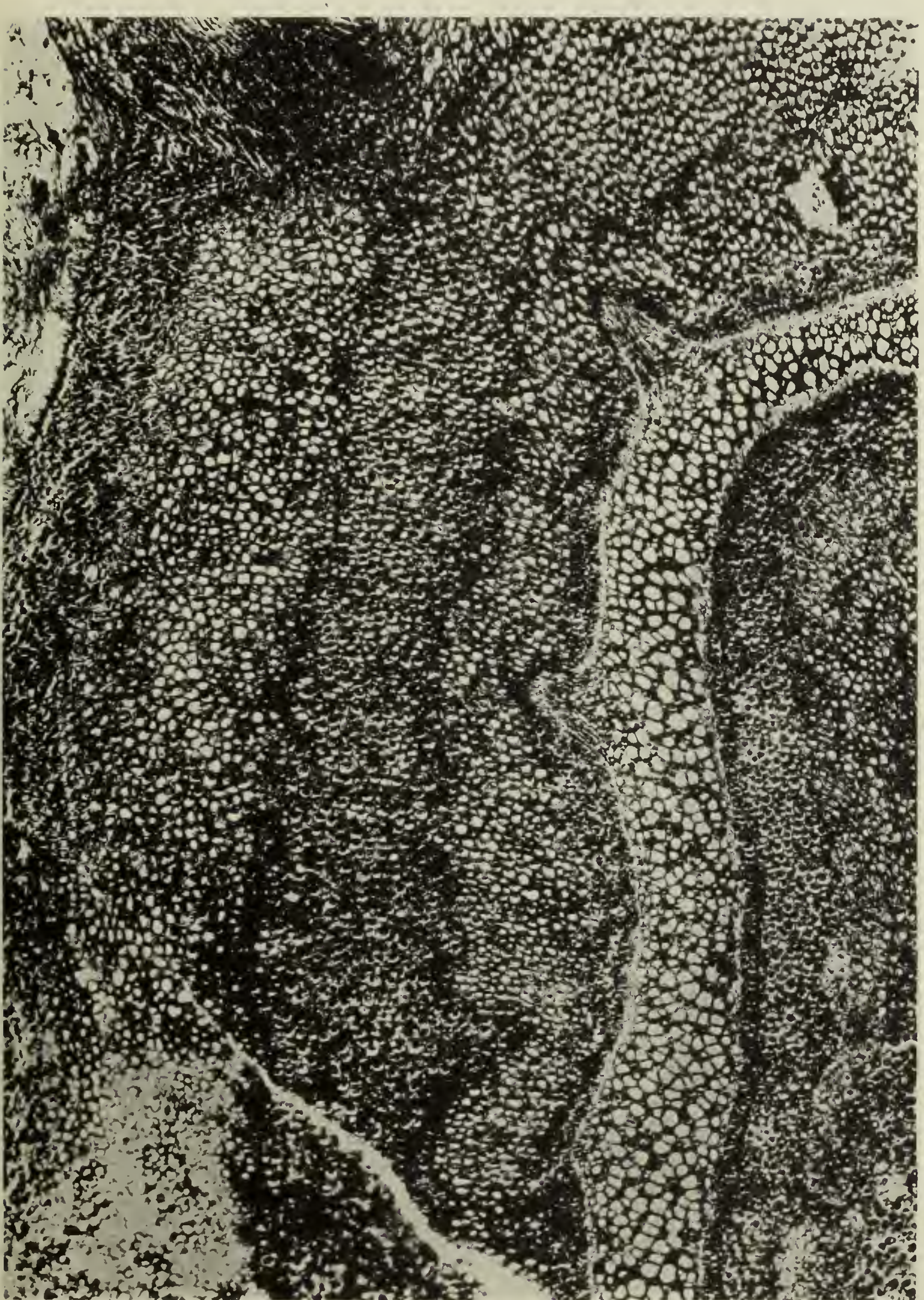
PLATE 12

Tempskya sp.

FIG. 15. An arc of stele in Pl. 9, stem *a*, showing the origin of two roots. Scales arise from the epidermis (top left) where also a large root emerges from the stem. Dense outer cortex is visible (top left) sharply differentiated from the sclerenchyma of the middle cortex which in its turn is distinct from the parenchyma with black crystalline inclusions of the inner cortex. The irregular sclerenchyma belt of the inner cortex lies outside the stele but separated from it by a thin layer of the parenchyma. The endodermis is somewhat blurred owing to the slight obliquity of the section but can be seen in places in the slide by focusing. Associated tangentially elongate cells are clear in the slide, obscurely seen in the figure (right, inside stele). ×35. V.51841*i*.



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